AM
1936
lu

Ludwig, Carl E.

Boston University

Graduate School

Thesis

Quasi-social Behavior in the Insect World

by

Carl Edward Ludwig

(B.S.E., Fitchburg State Teachers College, 1935)

Submitted in partial fulfillment of the
requirements for the degree of
Master of Arts

1936

H

Digitized by the Internet Archive
in 2016

https://archive.org/details/quasisocialbehav00ludw

AM
1936
lu

CONTENTS

Page

Introduction. 1

I. Rudimentary Social Behavior Among the Orthoptera. .3

1. Family Blattidae. 3
2. Family Gryllidae. 3

II. Rudimentary Social Behavior Among the Dermaptera. .7

III. Rudimentary Social Behavior Among the Embioptera. .13

IV. Rudimentary Social Behavior Among the Zoraptera. . 15

V. Rudimentary Social Behavior Among the Hemiptera. . 17

1. Family Scutelleridae. 18
2. Family Pentatomidae. 22
3. Family Aradidae. 24
4. Family Reduviidae. 25
5. Family Tingidae. 26
6. Family Cyndidae. 28
7. Family Belostomidae. 29
8. Family Aepophilidae. 29
9. Family Membracidae. 30

VI. Rudimentary Social Behavior Among the Coleoptera. .31

1. Family Scarabaeidae. 31
2. Family Passalidae. 34
3. Family Tenebrionidae. 36
4. Family Silvanidae. 37
5. Family Ipidae. 40

Page

6. Family Platypodidae. 41

VII. Rudimentary Social Behavior Among the Hymenoptera...... 44

1. Family Tenthredinidae. 44

2. Family Bethylidae. 45

3. Family Vespidae. 46

a. Masaridinae. 47

b. Eumeninae. 47

c. Zethinae. 49

4. Family Sphecidae. 50

5. Family Bembicidae. 51

Conclusion. 53

Digest. 54

Introduction

The evolution of social life in the insect world can be readily traced in the quasi-social insects. In a few exceptional cases, notably among the wood-boring insects, ~~there is~~ we find the first indications of social or colony life. Examples of incipient social life occur in some of the roaches, the wood-boring beetles, and certain species belonging to the order Zoraptera, in which there appears to be a primitive caste system.

Some insects, for example certain species of plant lice, are frequently found living and feeding together in large numbers, no doubt merely due to the fact that the eggs were laid in a mass or close together. In others, larvæ or adults or both, form large aggregations. The individuals, of which these aggregations are made up, plainly show that they ~~are attracted to each other~~ occur in groups for other reasons than a common place of birth or a suitable feeding ground. For example, according to Uvarov (1928), the nymphs of certain grasshoppers ~~according to Uvarov (1928)~~ ~~very plainly show the~~ have the same instinct ~~of~~ as certain gregarious vertebrates of "following the leader". Other aggregations, such as the larvæ of tent caterpillar moths, and the adults of certain species of coccinellid beetles, are protective. In certain other groups of insects, for instance

the Odonata and Lepidoptera, adult aggregations are, in at least a few instances, formed in connection with migration. Still other aggregations, for example those of some Ephemerida, Diptera and Hymenoptera, are primarily concerned with mating. But in practically all of these cases, the aggregations thus formed are more or less temporary and do not involve any association of parents and offspring, and therefore probably do not represent evolutionary stages in the development of the complex insect societies as we find them in ants, bees, wasps and termites. However, the probable evolutionary stages of insect societies are clearly shown by the social behavior of the "quasi-" or "subsocial" insects, since they form a connecting link between the strictly solitary and truely social insects. As we shall see, many of these quasi-social insects have not gone much beyond a very rudimentary social organization, but in a few instances, we have a social organization which closely approaches that of true insect societies.

I. Rudimentary Social Behavior Among the Orthoptera.

Until very recently, relatively little detailed organized information had been assembled on the subsocial behavior of the Orthoptera; nevertheless, some very interesting observations have been made on the roaches (Blattidae) and the crickets (Gryllidae).

In the family Blattidae, one of the best examples showing a vague approach to the social habits of the termites, is *Cryptocercus punctulatus*. Snyder (1924) and Wheeler (1928b) have made observations on this particular species and have found that the parents and offspring live together in colonies in the dead sap-wood of stumps and logs, eating their way through like termites. *Cryptocercus punctulatus* occurs in the Atlantic States from the Catskill Mountains to Georgia and then west to Kentucky. Cleveland (1934), while working on the protozoa of *Cryptocercus*, made observations concerning its social behavior which confirm those by Wheeler. Cleveland found this roach living in the same situations as those noted by Wheeler, but he often found more than one colony living together in the same log. The colonies of *Cryptocercus* are exceedingly small. Cleveland found that the colonies usually consisted of an adult male and female with fifteen or twenty nymphs, the largest of which ~~were~~ are less than half the size of the adults. It has

also been shown by Shelford (1906) that another species of the family Blattidae, *Pseudophoraspis nebulosa*, which occurs in Asia, is subsocial. Shelford captured a female of this species in Sarawak, Borneo, and found numerous young larvae clinging to the under surface of her abdomen. This clinging to the mother is of survival value to the young during their first few moults ~~and~~ until they are able to secure food for themselves. Another very interesting method by means of which the young obtain protection is shown by *Phlebonotus pallens*. According to Shelford (1906), there is in the Hope Museum a female of this species with the following label attached: - "Ceylon, J. Staniforth Green. Carries its live young beneath its wing-cover. 1878." Shelford has found living females of this species and has examined them very closely. The tegmina are large and convex, the wings being rather small and the abdomen concavely depressed above, so that a brood-chamber is formed under the tegmina in which there is sufficient space to accommodate several young larvae.

There are two other species belonging to the Blattidae, the social behavior of which needs further investigation. Wheeler (1928b), while in New Zealand, noticed that the roach, *Polyzosteria novae-seelandice*, ~~that~~ has very similar habits to those of *Cryptocercus punctulatus*. In the case of an-

other genus, Dasypoma, which occurs in North America, Snyder (1924) found the males and females living together with their young in rotten wood.

As regards the family Gryllidae, there is only one genus, Gryllotalpa, commonly known as the mole-cricket, which shows a vague approach to social life. This insect is rarely seen, because it lives almost entirely underground and hence its habits are but little known. One of the species, Gryllotalpa hexadactyla, has been studied by Morse (1920). It lives in damp soil and the female lays her eggs in clutches of from sixty to one hundred in lateral chambers which are just large enough to permit the adult female to turn around. On one occasion, Morse was fortunate enough to find a female mole-cricket among a numerous brood of her young ones.

Edward Step, in his well-known book entitled, "Marvels of Insect Life", has the following to say concerning the mole-cricket Gryllotalpa vulgaris.

"The female lays her eggs, to the number of two to four hundred, in a special cell excavated just below the surface, and is said to look after the needs of her brood until they cast their first skin, when they are able to look after themselves, and each starts burrowing for itself. It is calculated that their development from the egg to sexual maturity is spread over four years. The

mother is said to have to keep them away from the male, who otherwise would eat them."

Reuter (1913) found that in the case of Gryllotalpa gryllotalpa the mother cricket also cares for her eggs and young nymphs in a special underground chamber. The nest is made up of a number of passageways leading in all directions, so that it is difficult to locate the brood chamber. Both Kirkaldy (1903) and Reuter (1913) mention the interesting obersvations made by Goedaert (1662) on the social behavior of this particular insect. Goedaert states that the female mole-cricket takes particular care of her eggs, raising the nest in hot and dry seasons so that the young almost touch the roof of the burrow and in this way get the benefit of the sun's heat. But if the air is cold and moist, the mother lowers the nest, the females of these insects thus acting as unceasing sentinels during the time the eggs hatch and also during the development of the young.

II. Rudimentary Social Behavior Among the Dermaptera.

The Dermaptera, commonly known as earwigs (Forficulidae), are among the more primitive insects showing subsocial tendencies in their life-history. The earwig is found all over Europe, but seldom in extreme numbers. In North America, species belonging to the order Dermaptera are fairly common in our southern states and occur in smaller numbers along the Atlantic seaboard as far north as Maine. The life-history and habits of three species of Dermaptera have been studied, and it has been found that each one of these species is quasi-social.

Bennett (1904), who studied one of the three species (Anisolabis maritima) in Cold Springs Harbor, N. Y., gives an excellent account of the egg-laying habits of the female and maternal care for her young. The female, at the time of egg-laying, digs a small subterranean chamber, about one-half an inch deep and one inch wide. The chamber is usually hollowed out beneath a log or some other object which rests on the ground. The sand, excavated from the burrow, is carried to the outside in her mandibles. She also removes all sticks or pebbles which she encounters during the digging, so that the nest is free of all débris. The female is now ready to ~~deposit~~ lay her eggs. The eggs, when first laid, are about two millimeters in length, cylindrical

in form, and white, with a glossy, almost transparent, shell. The time required for the eggs to hatch depends upon the temperature and humidity, the average length of time being about seventeen days. The nymphs, when first hatched, are white, but soon turn black above and brownish below so that they resemble their parents very closely in color. Bennett counted about ninety eggs in an earwig nest which he found out in the open, but captive females, which he had under observation, never laid more than twenty-five. As soon as the eggs have been laid, the female ~~parent~~ picks each one up and cleans it by rolling it around in her mouth. After this process, the eggs are clean and glossy and she now places them in a pile and then stands guard over them. Bennett noted that in captivity, the females moved their eggs several times from place to place, carrying them one at a time. After the eggs have hatched, the female continues to guard her young for a few days. About this time the nymphs leave the parental nest to seek food for themselves, but it is dangerous for them to return, for at this stage they are sometimes eaten by their mother. Bennett (1904), found that one of his captive females reared as many as four broods during a single summer.

The European earwig (Forficula auricularia), which also occurs in certain parts of North America, has been

studied at Newport, Rhode Island, by Jones (1917) and in Oregon, by Fulton (1924). Fulton carried out some interesting experiments on the maternal care of the eggs and the young. After filling several cages with sand, he secured a number of female earwigs, together with their eggs, out-of-doors, and placed each female in a separate cage. The eggs, belonging to each female, were then scattered about in her compartment, whereupon the female almost immediately started to collect her eggs, one by one, placing each near a small egg group accidentally formed during the process of scattering. Within less than half an hour, each female had collected all of her eggs in one pile and was proudly standing guard, rolling one by one around in her mouth. Fulton had no cage for one of the earwig females and therefore placed her and eggs in the cage of another female. ~~And~~ Fulton was soon able to observe the following: "At first each female began gathering eggs without noticing the other and two small piles were started. Everything was moving along peacefully until the smaller earwig of the two started out to hunt for more eggs and came upon the other pile. She was about to remove one of the eggs when the larger female discovered her. A lively fight followed, with reckless disregard for the eggs, which were scattered in all directions. Each female tried to nip the other in the abdomen with her

forceps. They went round and round without inflicting any serious injury until the smaller one became frightened and fled.

"They again went about the business of gathering eggs but every time their paths crossed, there would be a fight. After several bouts, the smaller happened to find refuge in the small cavity which I had prepared in the sand. I left this cage for a time and when I returned the larger earwig had all the eggs piled except about a dozen which the smaller one had with her in the cavity. Presently the small earwig came out and approached the other pile of eggs cautiously, and attempted to remove one from the edge of the pile, but was driven away. She tried this several times and was driven away more vigorously each time. Finally the larger earwig followed her clear into the cavity and seemed about to settle the dispute there when suddenly the pursuer discovered the small pile of eggs. She immediately abandoned the fight and ran away with an egg to her own pile. From then on she paid no attention to the smaller earwig until she had removed every one of the eggs from the cavity and added them to her hoard, after which she stayed to defend it. The smaller earwig when last seen was making a frantic effort to dig into the sand, completely vanquished."

Fulton also made some important observations on the

solicitude shown by the mother ~~of~~ toward the nymphs. The latter crawled under and over their mother in a very similar way as do newly-hatched chicks about the mother hen. The female occasionally picked up one of her young with her palpi and placed it in a different position. On several occasions Fulton saw several young earwigs reaching up and touching the mouth of the mother as if trying to obtain food, for they piled up on top of each other and seemed very eager to touch her mouth. In fact, they appeared so eager, that Fulton suggests that the female was actually feeding them something by regurgitation. The young always stayed within two or three feet of the mother when newly hatched. When pieces of insects were placed in the cage, the female came out and carried the food into her nest. She ate some herself and then fed some to her young. She also carried pieces of dandelion offered her into the nest and placed it where the young could feed upon it.

Fulton also tested the ability of the female earwig to protect her young from enemies, by placing a ground beetle (Carabidae), which was about half an inch long, into the cage. The mother earwig did not hesitate to assail the beetle so violently that the intruder fled to a hole in the sand. A predacious larva of another ground beetle was then introduced into the cage with similar results. During the

encounters of their mother with the intruder, the young invariably fled to a safe place. However, as soon as she had succeeded in driving away the larva, the young earwigs immediately returned and huddled about their mother.

Similar observations have been made on another species of earwig (Anechura bipunctata) by Stäger (1919) in Europe. Stäger did most of his work out in the open and very interestingly describes the behavior of the female of this earwig and her offspring as follows in German. "Whenever I turned over a stone of a certain size on an expansive Alpine terrace, I found the mother among a brood of about fifty to sixty young larvae. Before my eyes the slender, graceful creatures squirmed as they tried to hide themselves in the small cavity, which the mother had dug in the earth for her brood. And she, herself, did not flee, but, on the contrary, sheltered her young with her own body and with her pincers snapped at the fingers of the intruder, who attempted to seize her. If I resorted to force and separated the mother from her brood, then she hastened back immediately to the cavity and continued to defend her young. However, when I pushed one of the small larvae aside, the mother followed shortly afterwards, seized her kidnapped offspring with her mandibles and carried it back into the nest."

III. Rudimentary Social Behavior Among the Embioptera.

This is a comparatively small order of about fifty-six described species confined to the tropical regions. According to Wheeler (1928b), these insects are even more primitive than the earwigs. They live in small colonies in silken webs which are spun in cavities of the soil under stones or on the bark of trees. Several biologists have made observations on the habits of the Embioptera. The more important work on this group of insects, includes that of Westwood (1837), Perkins (1897), Melander (1902), Imms (1913), and Wheeler (1928b).

Imms (1913) discovered a large species, Embia major, nearly an inch long, in the Himalaya Mountains and has published a detailed account of its habits. Embia major is the largest species of the family Embiidae and is frequently found under stones that are scattered over the hill-sides and open valleys in the Naini Tal district. The nests are made up of silken tunnels and vary as to size and form, the size of the nest depending upon the number of insects living together. The largest colony found by Imms consisted of twenty-one individuals. The number of eggs laid by each female varies between about sixty and one hundred. The eggs are placed within a silken tunnel in a rather irregular heap. The care which the mother bestows on the

larvae has been extensively studied by the same author. The female is very devoted to her eggs and young. She usually tries to hide her eggs from view by means of her body. When becoming alarmed and driven away for some reason, very little time elapses before she comes back, to again take her position over her eggs. As soon as the young larvae are hatched, they stay with the mother, which guards and conceals them while they are in this stage of development. Imms placed a female and her brood in a small glass trough, so as to be able to observe their social behavior more readily. When he separated the larvae from their mother, he found that the larvae had invariably rejoined the mother by the following day. The larvae begin to wander away from the female as they approach their second stage in development and construct small tunnels of their own.

IV. Rudimentary Social Behavior Among the Zoraptera.

According to Wheeler (1928), the order Zoraptera remained unknown till 1913, when it was established by Silvestri on a single species of the genus *Zorotypus*. Since then, a number of additional species have been described from tropical countries - Africa, Ceylon, Java, Costa Rica, and Florida.

Caudell (1920) and Snyder (1924) have made some observations on several species of *Zorotypus*. All the species studied are very active little insects living under conditions very similar to those in which termites are found and the adults closely resemble termite young.

Caudell (1920), who studied *Zorotypus snyderi* and *Zorotypus hubbardi*, has the following to say concerning these two species: "Both species of *Zorotypus* are social insects, occurring in colonies of various sizes. They generally occur near Termites, but are not mingled with them and are probably never really inquilinous with them, as was at first thought probable, due to their usual proximity to white ants and their frequent occupancy of their galleries."

Snyder (1924) found that the species of *Zorotypus* which he studied have apterous as well as winged reproductive forms. The winged individuals get rid of their

wings before rearing their young in the same manner as the lower termites. The young are reared in runways under the bark of dead trees and logs in moist places.

V. Rudimentary Social Behavior Among the Hemiptera.

It is a generally known fact that the phytophagous species of the order Hemiptera ~~deposit~~ lay their eggs on certain food plants, and then leave the resulting young to shift for themselves. However, in some species of Belosto~~ma~~tidae, the female catches a male and lays her eggs on his back where they are protected to a certain extent until they hatch, but it is reported, that in these cases of parental care, the male is an unwilling partner.

Hussey (1934) and Bequaert (1935) have recently published a list of the known cases of parental care among the Hemiptera. According to these authors, parental care has apparently developed independently in the following nine families: ~~of Hemiptera~~:

Scutelleridae:	*Tectocoris diophthalmus*.	Australia.
	Cantao ocellatus.	India to Papua.
	Pachycoris fabricii.	West Indies.
	Pachycoris torridus.	Central and South America.
Pentatomidae:	*Meadorus griseus*.	Europe.
	Phloeophana longirostria.	Brazil.
	Phloea corticata.	Brazil.
	Chlorocoris atrispinus.	Guatemala.
Aradidae:	*Neuroctenus pseudonymus*.	North America.
	Ctenoneurus hochstetteri.	New Zealand.

Reduviidae: *Endochus cingalensis*. Ceylon.
Rhinocoris albopunctatus. Africa.
Rhinocoris albopilosus. Belgian Congo.
Tingidae: *Gargaphia solani*. North America.
Gargaphia tiliae. North America.
Cydnidae: *Sehirus sexmaculatus*. Europe.
Belostomidae: *Lethocerus americanus*. North America.
Aëpophilidae: *Aëpophilus bonnairei*. Western Europe.
Membracidae: *Platycotis vittata*. North America.

The following is a brief résumé of the parental care observed in the species enumerated above.

Scutelleridae

Montrouzier (1855) was apparently the first one to call attention to the social behavior of the insects belonging to this family.

Tectocoris diophthalmus (= *T. lineola*), an Oriental species, was observed by Dodd (1904). The female lays her eggs in a mass on an upright twig and takes a position above the eggs, and, according to this author, never leaves them. When an object is brought near her from the side, she bends towards the threatening object as if to shield her eggs. Ballard and Holdaway (1926) who have also studied the life-history of this species have confirmed Dodd's

statements in general. Contrary to Dodd's report, both of these observers found that the female sometimes leaves her eggs and sits on a nearby leaf, acting as though she were still on the egg-mass. They also noticed that one of the females moved in all directions, while three chalcids were trying to dodge her during their attempts to parasitize the eggs. Ballard and Holdaway found this insect most accommodating, for the female can be removed from her egg-mass and placed on a leaf nearby, while the eggs are counted, and then replaced on the eggs.

An~~other~~ Oriental species, Cantao ocellatus, has been observed guarding the eggs and young nymphs by Ayyar (1920). After the female has deposited her eggs on a leaf of one of the euphorbias, she stands guard over her eggs until they hatch. During this time she takes no food and if an intruder approaches she acts precisely as Tectocoris diophthalmus. She vibrates her antennae and brings her body closer to that side of her brood which is being threatened. The female is not large enough to cover the whole egg-mass; hence the ~~outer eggs develop a dark tinge~~ exposed eggs can easily be parasitized by chalcids which causes these eggs to develop a dark tinge. Ayyar collected a mother with her egg-mass and noticed that minute black wasps emerged from the dark-tinged eggs. Takahashi (cf. Bequaert, 1935), who also studied Cantao ocellatus, describes the behavior of the

female as follows: "With the tip of her abdomen the female lays ten or twenty or more eggs on the under side of the leaves of certain trees. Generally eggs of Hemiptera are not white, but those of Cantao ocellatus appear so. The female oviposits only once and the eggs are placed in a single row. After she has laid the eggs, she places her abdomen over them, extends the antennae forward and stays there without moving, never leaving the spot......Before they lay eggs, the females walk a good deal; sometimes they jump, at other times they keep quiet. When the insect is not moving or walking, it easily drops to the ground if touched with the point of a pin ....

"If approached, she moves her legs and antennae a little, and if touched with a pin or other object, she moves her body a little, but she never walks away nor drops to the ground. I have moved the antennae and legs and pressed them with a pin in many specimens, but they never left the spot and clung to the eggs. The female frequently lifts her head while sitting on the eggs, and sometimes she moves her legs to the left and right and cleans her antennae ....

"After the eggs have hatched the nymphs remain in the egg shells and do not take food nor move about. In other words, the nymphs stay under the maternal body. They

undergo two moults within about six days; a few days later they begin to move about, leaving the egg-shells and looking for food. This then ends the maternal protection; the nymphs feeding after the second metamorphosis."

Takahashi also noted the fact that the female does not leave her empty egg-mass after the nymphs have gone, but stays there and dies from hunger. He ~~also~~ performed some experiments and found that a female will readily adopt a strange egg-mass, strange nymphs, or even a batch of empty egg-shells. On the other hand, if a female has not yet oviposited, she will not stay with strange eggs or nymphs. Takahashi concludes that "the female of C. ocellatus cannot discriminate between her own eggs or nymphs and those that belong to another female and that in fact all females become dormant after the eggs are laid."

The behavior of Pachycoris fabricii, a West Indian species, has been observed by Barber (1925), who noticed quite a number of small dark-green nymphs spread over the surface of a leaf, on the under side of which he found a brilliantly colored female. When Barber shook the leaf slightly, the little bugs ran to the mother - which did not move - and hid under her body.

Similar habits have been observed by Hussey (1934) in connection with Pachycoris torridus. The female of

this species usually lays her eggs on the under-side of a leaf of a~~one of the~~ Paraquayan trees belonging to the family Euphorbiaceae. The female deposits her eggs in a flat plaque, each ovum glued to the surface of the leaf at its caudal end, the number of eggs ranging from about fifty to one hundred and fifty. The mother stands guard over her brood during the entire period of incubation and also during the first nymphal stage of the young, her body just about covering the egg-mass. As soon as the young emerge, they huddle under her in a mass. If the female is lifted from her place, she clings so tightly to her eggs that the latter are torn from the leaf.

Pentatomidae

Quite a number of instances of parental care have also been observed in the family Pentatomidae, the following being some of the more interesting.

The habits of *Meadorus griseus*, a common European pentatomid, were first studied by Modeer, whose Swedish account of their behavior was translated into German by Herbst (1786). Modeer relates that the eggs are laid in June on the common birch and number from about forty to fifty. The mother does not leave her eggs, except for brief periods while feeding, and can be removed from her egg-mass only by superior force. But in this case the

solicitude of the mother ~~for~~ toward her offspring goes even further, for as soon as the young hatch, she has also to protect them from any pentatomid males, which readily feed upon the young nymphs.

Phlaeophana longirostris (= Phloea paradoxa) has been studied in detail in Brazil, by de Magalhaes (cf. Hussey, 1934). The female and her brood are often overlooked because she closely resembles patches of lichens which grow on the tree. She covers from eight to twelve eggs with her body, which is closely applied to the tree. When the young nymphs emerge, they cling to the under side of the mother's abdomen and stay there until the last nymphal stage is reached. It has been suggested by de Magalhaes, that the nymphs are probably fed by the mother with some juice she secretes, because the proboscis of the nymphs at this time is much too short to pierce the bark for sap.

Very similar habits have been observed by Schiödte (cf. Bequaert, 1935) in the case of Phloea corticata.

Another American species, Chlorocoris atrispinus has been studied by Bequaert (1935), who found a female of this bug resting on the under side of the frond of a tree-fern. She showed no signs of fear and when Bequaert picked her up, he found fifteen small nymphs clinging to her body. The empty egg-shells were still on the frond

where the mother had been sitting and undoubtedly these nymphs had just emerged and had not yet started to feed.

Aradidae

Another family of Hemiptera which has been shown to have presocial habits is the family Aradidae.

According to McClure (1932), the female of Neuroctenus pseudonymus deposits her eggs in burrows, made by other insects, under the bark of dead trees. The eggs are found in masses of about ten to fifty in number. McClure observed some individuals belonging to this family feeding upon the juices of decay under the bark of a dead oak tree. Eggs, nymphs of all instars, and adults were present. McClure found that after the female had laid her eggs and departed, another adult, probably the male, crawled astride the egg-mass and remained. Upon hatching, the nymphs climbed on top of the empty egg-shells and remained under the guardian for two days. Then the adult left the nymphs, ~~which then~~ whereupon the latter began to scatter. Bequaert (1935) believes that McClure's surmise that the second adult was a male is probably correct, since he himself found that in the African reduviids, Rhinocoris albopilosus and Rhinocoris albopunctatus, as will be pointed out later, apparently only the male guards the eggs.

Another aradid, Ctenoneurus hochstetteri, has been

studied by Myers (1921) in New Zealand, who reports that the adults "are sometimes found carrying several first or second instar nymphs on their backs and sides in a manner comparable to that of Lycosid spiders. Considering the gregarious habit of the species, perhaps we should rule out maternal solicitude as an explanation; but it is significant that these young nymphs do not apparently cling to older nymphs which closely approach imagines in size."

Reduviidae

It is rather interesting that rudimentary stages of family life are even found among assassin-bugs (Reduviidae).

According to Kirkaldy (1904), Green observed that the females of several reduviids - e.g. Endochus cingalensis and allied species - remain near their egg clusters until these are hatched. The nymphs stay together on the same leaf and are guarded by the mother who keeps watch over them.

Rhinocoris albopunctatus, a common reduviid in in the Katanga District of the Belgian Congo, was observed by Bequaert (1935) guarding the egg-mass attached to a stem. The young nymphs remained with the adult for some time after hatching and Bequaert was surprised that in each case, it was a male that took care of the young, and not the female. Very similar observations were made by

Bequaert on Rhinocoris albopilosus, a closely related species. The eggs are attached to herb stems at a height of about thirty centimeters from the ground in single plaques containing about two dozen eggs, arranged in two to five irregular rows. The male stands over them with the venter almost touching the eggs, and if alarmed, he may run up and down the plant stem but does not fly away. Bequaert also saw the watchful male repulse chalcid wasps from the eggs which he was protecting. When Bequaert forced the male to leave the egg-mass, the male invariably returned to the eggs at the earliest opportunity. When an ant was placed on the egg-mass, the male moved away, apparently frightened by the movement of Dr. Bequaert's hand. However, the male soon returned and explored the egg-mass with his antennae until he accidentally came in contact with the ant, whereupon the bug viciously attacked the ant, piercing it with his beak and then dropping it to the ground. He then again took up his position over the egg-mass.

Tingidae

In this family, there are two North American species of the genus Gargaphia, the females of which exhibit maternal solicitude toward their eggs and young nymphs.

The social behavior of one of these species, Gar-

gaphia solani, was first observed by Fink (1915). The minute greenish eggs are deposited on the under side of leaves in circular masses of about one to two hundred. In this case the female occasionally leaves the eggs at intervals to feed, but returns to them promptly after she has satisfied her hunger. However, when the young nymphs commence to emerge, their mother does not budge from the nest. She ~~does this~~ remains there for several days, since not all of the eggs hatch at one time. The maternal care which is bestowed upon the young nymphs by this species is very interestingly related as follows by Fink: "When migrating from one leaf to another the female adult usually directs the way and with her long antennae keeps the nymphs together or rebukes any straggler or deserter. It is an interesting sight to observe the migration of a colony of more than a hundred nymphs, with the female adult hurrying from one end of the flock to the other, keeping them together and at the same time urging them in the right direction during the migration."

That the female keeps a watchful eye on the nymphs is shown by the following observation of Fink (1915). On one occasion, while he was watching the young nymphs feed, a ladybird beetle (Hippodamia convergens) approached the brood. The mother lacebug, who was guarding the brood at

the time, raised and spread her wings and made a dash for the intruder, and in this way succeeded in driving the latter from the feeding ground.

Gargaphia tiliae, the second species studied, has very similar habits, and has been extensively studied by Weiss (1919) and by Torre-Bueno (1935). Weiss found that the eggs are inserted in the lower leaf-surface of linden trees and occur in clusters of from sixty or less to about three hundred. The mother stands guard over the eggs throughout the incubation period and usually watches over the nymphs until they are full grown.

Cyndidae

All of the Hemiptera discussed in the preceeding paragraphs lay their eggs on leaves or bark of trees. Sehirus sexmaculatus, a European species, is quite different in this respect. Boselli (cf. Bequaert, 1935) found that in this case the female digs a small hollow underground and lays a compact mass of about one hundred to one hundred and twenty-five eggs which she firmly grasps with her legs. When disturbed, she remains motionless and devoted to her egg-mass, but if removed from the latter she becomes very restless until she regains possession of them. After such an event, she can usually be seen tucking the eggs under her body. The newly hatched nymphs stay with

with their mother throughout the first instar.

Belostomidae

An interesting case of parental care has been reported by Hoffmann (1924) in connection with J. R. Parker's studies of the giant water-bug, Lethocerus americanus. Parker found a male and a female guarding some eggs on the bank of a small pool. The eggs had been glued to the grassy bank about a foot above the water. As Mr. Parker approached the eggs, the male made a dash for the water but he captured him. Parker then went still closer to the eggs and the female quickly assumed a fighting position with her front pair of legs outstretched and ready for action. When an object was brought within reach of her front legs, she struck viciously at it. Parker put a stick in front of her, whereupon she seized it and clung to it long enough to be put into a cyanide jar.

Aëpophilidae

The instinctive solicitude of the female Aëpophilus bonnairei, ~~for the~~ toward her young, has been observed by Keys (1895 and 1914). This bug lives under stones on the coast of western Europe, below the high-water mark, and is semi-aquatic. Keys studied the habits of this species in breeding cages, where he often found a female with all her

immature nymphs circled about her, heads toward the center, on the under side of a stone. Whenever he lifted a stone with an adult and her brood under it, the female immediately warned her young with rapid taps of her antennae, and the nymphs then immediately scampered to the opposite side of the stone.

Membracidae

Some interesting observations in regard to the parental care of one of the membracids, Platycotis vittata, were recently made by Beamer (1930), who found several females of this species, each one standing guard over some nymphs. When, in one instance, a wasp approached the nymphs, she was driven away by the mother, and finally departed. The female then flew to her young and apparently examined them to see if any had been injured; then making sure all was well, she returned to her former position.

VI. Rudimentary Social Behavior Among the Coleoptera.

Although the Coleoptera comprise one of the largest orders of insects, only the following six families exhibit subsocial propensities, according to Wheeler (1923).

Scarabaeidae: *Scarabaeus sacer*
Sisyphus schoefferi
Copris hispanus
Copris lunaris
Minotaurus typhoeus
Passalidae: *Passalus cornutis*
Tenebrionidae: *Phrenapates bennetti*
Silvanidae: *Coccidotrophus socialis*
Eunausibius wheeleri
Ipidae: *Pterocyclon mali*
Pterocyclon fasciatum
Xyleborus xylographus
Platypodidae: *Platypus compositus*

Scarabaeidae

Most of what is known concerning the social propensities of the Scarabaeidae we owe to the well-known French entomologist Fabre (1918), who made extensive observations on several species of dung beetles, one of the subdivisions of this large insect family. Among others, Fabre studied

the behavior of the sacred scarab, *Scarabaeus sacer*. When the female of this species is ready to lay her eggs, she makes a pellet of sheep dung and rolls it into an elliptical chamber which she has previously dug out in the ground. She makes a hole in one end of the pellet, lays a large egg in it, and then closes the hole again. The female departs and proceeds to dig another chamber and provisions it in the same manner. The hatching larva consumes the inner mass of the pellet, pupates within it, and later emerges as an adult beetle from the underground chamber. This insect, however, is not social in the strict sense. But in a smaller allied species, *Sisyphus schoefferi*, Fabre observed the male beetle assisting the female. The female choses her mate in early spring at the beginning of the breeding season. Both parents take part in stowing away the food for their prospective young. They mould the dung into a small ball and carry it to a spot nearby. The female now commences to dig a hole, while the male stands guard over the pellet. When she has completed the chamber, the male gently lowers the pellet to the female below. The male then creeps out of the hole and sits patiently at its entrance, allowing no intruder to enter. After the female has deposited her egg, she emerges from the hole and is again joined by the male to repeat the performance.

Fabre found an even greater degree of cooperation between male and female in the case of *Copris hispanus* and *Copris lunaris*. The male and female of *Copris hispanus* always work ~~in~~ together while ~~cooperation in~~ excavating the chamber and filling the latter with dung. The pellet, in this case, has the form of a smooth ellipsoid and is as large as a turkey's egg. ~~The~~ After a sufficient amount of dung has been collected, the male ~~then~~ leaves the chamber and never returns. The female now cuts the large pellet into four smaller ones and lays an egg in each. She remains in the underground chamber for about four months, keeping the pellets free from vegetative growths, while the larvae are developing. At the end of August, the young beetles release themselves from their enclosures and make their way to the surface with their mother. In *Copris lunaris*, whose habits Fabre also studied in much detail, the male remains in the chamber with the female and assists in the manufacture of the pellets. Owing to his assistance, according to Fabre, there are twice as many pellets as in the case of *Copris hispanus*. The male and female stay with the pellets while the larvae are developing within them. Shortly after the young beetles emerge, they make their way to the surface with their parents.

Another scarabaeid beetle, exhibiting a considerable degree of cooperation between the male and female is

Minotaurus typhoeus. According to Fabre (1911), the beetles mate in March and dig a tunnel straight down into the ground to a depth of five or more feet. As in the preceeding case, the female does all the digging, but here the male carries away the débris. After the female has deposited an egg in the sand at the bottom of the burrow, the male collects sheep dung, molds it into pellets, and then lowers them down the shaft to the female, who breaks them apart and piles the fragments over the egg. The female then digs a few galleries from the main shaft, deposits an egg in each and provisions them in a similar manner. The male, after having helped the female complete the birthplace of their prospective young, then leaves his mate and dies.

Passalidae

The family Passalidae, another subdivision of the Lamellicornia, likewise contains a number of subsocial species. They are large, jet-black, flattened beetles and are abundant in the tropics of both hemispheres. They are represented in the United States by only one species, *Passalus cornutus*, which ranges as far north as Massachusetts and Illinois. The first one to study the habits of this common and conspicuous beetle was Ohaus (1899-1900), who found them living in colonies in rotten logs, each

colony consisting of an adult male and female with their progeny. The beetles excavate large galleries, pulverizing the wood and apparently treating the particles with some digestive enzyme, so that they can be digested by the larvae, which slowly follow their tunneling parents. The young larvae soon die when removed from their parents, because they are unable to break down the wood with their mouthparts. The broadly elliptical, greenish eggs are guarded by the parents. When the larvae hatch, the adults provide them with plenty of food. Ohaus has observed the adults protecting the pupae and feeding the young beetles till their chitinous integument is completely hardened.

While Dr. W. M. Wheeler (1921) was in Trinidad and British Guiana, he made a few observations on several species of Passalus which are very common in rotten logs throughout the jungle. He describes the social behavior of these beetles as follows: "Just under the bark the beetles make large, flat cavities, which are later often occupied by the fungus-growing ants of the genera Apterostigma, Myrmicocrypta and Cyphomyrmex, and evidently furnish just the right places for their more or less globular gardens. In each of the Passulus colonies examined during July and August there were only two adult beetles, usually accompanied by a troop of larvae varying little in size and

evidently belonging to a single brood. In one log, however, we found a pair of beetles guarding a batch of about forty large, olive-green, broadly elliptical eggs, some of which had just hatched. The young larvae closely resembled the older individuals in the structure of the peculiarly modified paw-like metathoracic legs, which are rubbed over the finely ridged middle coxae during stridulation, but the hairs on the body were conspicuously longer and coarser."

Wheeler and Bailey (1920) have published an account of the stridulatory organs of the young larvae and the adults of Passalus, and suggest that the colony is kept together by the shrill notes given off by various members at different times. In this way, a colony can easily be detected by listening for these shrill sounds in decaying wood.

Tenebrionidae

A subsocial species, Phrenapates bennetti, has also been discovered in the family Tenebrionidae. Ohaus (1899-1900) encountered this beetle in Ecuador and found some evidence for placing it among the social beetles. The adult parents gnaw a narrow, cylindrical gallery, about a foot and a half long, in the wood of the silk-cotton tree (Bombax). At definite intervals along the burrow, one finds spacious chambers that are destitute of any

debris what-so-ever. Ohaus found that each chamber contained an egg or one or two larvae. Whenever larvae were found occupying the niches, elongate shavings could be seen stored near them, apparently placed there by the parents for the emerging young to devour. The larvae were found to be of all sizes, so Ohaus concluded that the female must lay her eggs at rather long intervals. The larvae resemble those of our common meal-worm (Tenebrio molitor), but are white in color.

Silvanidae

During the summer of 1920, while Dr. Wheeler (1921) was working with Prof. I. W. Bailey on the myrmecophytes of British Guiana, he discovered two species of beetles (Coccidotrophus socialis and Eunausibius wheeleri) of such unusual social habits, that he devoted considerable attention to their behavior. These beetles live in enlargements of the petioles of a tropical Tachigalia tree, which is also inhabited by numerous species of ants. Both the beetles and the ants cultivate coccids in the hollow petioles, and with the beetles and coccids there are several associated parasitic or synoeketic insects. Since both Coccidotrophus socialis and Eunausibius wheeleri have very similar habits, it will suffice to discuss the behavior of the former, which Dr. Wheeler studied very intensely.

Coccidotrophus socialis varies in size from three

and five-tenths to four and five-tenths millimeters, and, when mature, has a very shiny appearance. As a rule, the adult beetles enter petioles which have been previously occupied by other beetles or ants. Usually a male and female enter together but it has been observed that one may enter alone and is joined later by another of the opposite sex. The adults then remove the loose pith or the remains of previous tennants by pushing this debris into the pointed ends of the cavity with their flattened heads. Wheeler found that the beetles live on the outermost layer of pith and strips of nutritive parenchyma which contains an amber-colored substance. Coccids now begin to appear, entering the petiole and taking up their positions along the strips of nutritive tissue. The frass and feces of the beetles is carefully deposited along ridges where it does not obstruct the nutritive parenchyma.

The female deposits her eggs along the ridges of frass but lays only a few at a time, so that larvae in all stages of development are found in the same colony. The larvae run about in the cavity and feed on the same tissue as the parents. The colony now consists of the parents, about one or two dozen larvae, and about the same number of young or half grown coccids. The mature larvae construct cocoons of minute particles bitten out of the plant tissue,

creep into ~~it~~ them and close the opening from the inside. When the young beetles hatch, they remain in the same petiole and soon begin to produce young. The colony reaches its climactic stage when it consists of several dozen beetles of both sexes and numerous larvae and pupae in all stages of development. While this is going on, the coccids are also increasing in number, so that the petiole cavity gets quite crowded. When the population becomes too dense, some beetles leave the colony and establish a new one in another petiole of the same or other tachigalias.

Wheeler noticed that when an adult beetle comes upon a coccid, it stops immediately and seems at once to become excited. It begins to stroke the coccid's posterior end and may continue this for an hour or more without getting any response. Whenever the coccid emits a droplet of sweet excrement from the anal orifice, the beetle greedily swallows it. It may then continue to stroke the same coccid for hours without getting any more liquid, but it apparently does not know enough to seek another. The larvae, regardless of age and size, likewise solicit and receive food from the coccids by tapping them with there antennae.

Wheeler concludes his interesting account of these beetles as follows: "The merely gregarious habits of the adults and larvae of the northern and cosmopolitan Cucujids

have become more definitely social in the Tachigalia beetles, and their toleration of alien insects has increased; the feeding of the ancient Cucujids on various vegetable substances has become specialized to the point of concentration on a particular tissue of a particular plant and both adult beetles and larvae have become coccidophilous."

Ipidae

The habits of several genera of ambrosia beetles of the family Ipidae (=Scolytidae), have been investigated by Hubbard (1897 and 1906) and by Hopkins (1898). The name "ambrosia beetles" is derived from a term applied by Schmidberger to the fungi which they cultivate as nourishment for their larvae and themselves. They are small, cylindrical, black beetles which occupy galleries in the trunks and branches of trees. Hubbard, who studied the habits of these beetles for the United States Department of Agriculture, worked on two of our North American species: Pterocyclon mali and Pterocyclon fasciatum. The adult female, assisted by the male, digs a burrow which extends far into the wood. The eggs are deposited singly in round pits which she hollows out in the burrow. She then surrounds each egg with material from the fungus bed which she has already prepared and upon which the fungus has begun to sprout. The hatching larvae eat the ambrosia growing on

the chips of wood and then lie curled up in the pit for a while. As they grow, they deepen their pits by means of their jaws, until the cradles slightly exceed the length of the larvae. The wood is not digested by the larvae, but is passed through the intestine and is excreted in the form of pellets. The larvae frequently clean their pits of débris, which is collected and thrown out by the mother. Hubbard found that the mother beetle constantly looks after her young and guards them with jealous care. Each cradle is closed with a piece of fungus ~~and~~ which is renewed by the mother as soon as the larva has eaten it. The larvae soon develop into adult beetles and then begin to wander about the galleries.

Another ambrosia beetle, Xyleborus xylographus, has been studied by Hopkins (1898), who found two females - instead of one - excavating a gallery together; one was doing the digging, while the other guarded the entrance and expelled the frass. Xyleborus xylographus is polygynous, one male usually consorting with several females. Each colony of these beetles, according to Hubbard, has a sort of death chamber into which any dead members of the colony are placed.

Platypodidae

The beetles belonging to this family are also known

as ambrosia beetles and were formerly included among the Ipidae. They, like the beetles of the preceding family, cultivate fungi as food for themselves and their larvae. The great majority of the species are tropical, living in drying or recently felled trees. A remarkable social organization that ~~in the case~~ of Platypus compositus was studied by Hubbard (1897 and 1906) and Hopkins (1898). This species usually excavates its galleries deep into the heartwood of large trees. Unlike the colonies of the Ipidae, those of Platypus compositus usually consist of many males and a very few females. When a female is ready to mate, violent sexual combats take place among the males. As a result of these combats, severed appendages of the vanquished can often ~~only~~ be found strewn about the galleries. The eggs, numbering from about one to two hundred, are laid ~~deposited~~ in clusters of ten to twelve. The young, which require approximately six weeks for their development, wander about the galleries and feed upon the fungi which grow on the walls. Hubbard observed that the older larvae show a considerable degree of consideration for the eggs and younger larvae, for they take great care to avoid them as they move about in the galleries.

Each species of ambrosia beetle, according to Wheeler (1923), grows its own peculiar fungus in a pure culture,

irrespective of the tree it may select for its burrows. Some entomologists believe that the female carries the spores from the chambers, in which she passed her larval and pupal stages, to the new burrows in a kind of basket consisting of one or more dense tufts of long curved hairs on top of her head, while others have suggested ~~entomologists believe~~ that the female carries the spores in the fore part of her stomach and is thus able to infect the walls of her new galleries.

VII. Rudimentary Social Behavior Among the Hymenoptera.

Among the Hymenoptera, we find a gradual transition of the parental care from species which merely provide a protected cell provisioned with paralyzed insects to species with an elaborate communal organization in which the young are cared for and fed by members of the colony.

The first stage in the evolution of presocial Hymenoptera is that of "mass provisioning", the female wasp or bee constructing a cell and provisioning it with an amount of food sufficient to enable the future larva to develop, without paying any further attention to the latter. An advance upon this type of parental care is that of "progressive provisioning". The larva in this case being fed from day to day.

In the Eumeninae, a subfamily of wasps, we find both of these methods of feeding the young, some species practicing mass-provisioning, while others feed their young in the same way as altricial birds (progressive provisioning).

The following five families among the Hymenoptera represent incipient stages of family life. ~~are known to rear their young by the second of the two methods just discussed.~~

Tenthredinidae

The habits of Perga lewisii, a Tasmanian sawfly, have been studied by Lewis (1836), who found that the eggs, about

eighty in number, are placed transversely in a longitudinal incision between the two surfaces of a Eucalyptus leaf. The mother remains on this leaf till the eggs have hatched, and then stands guard over her brood with outstretched legs, thus sheltering them from the heat of the sun, and protecting them from the attacks of parasites and other enemies. These observations of Lewis have recently been confirmed by Froggatt (1918).

Bethylidae

Bridwell (1920), who studied Scleroderma, a genus belonging to the Bethylidae, found that these insects show a definite approach to social conditions. Scleroderma is dimorphic, each sex being represented by a winged and an apterous form. These insects normally feed on cerambycid larvae, but have also been seen feeding on hymenopterous and dipterous larvae. When the female is ready to oviposit she seizes a larva, which is usually many times larger than herself, stings it repeatedly until it is paralyzed and then places her eggs on it. She now feeds upon the larva herself, biting it in several places and sucking the juices that exude from the wounds. As soon as her eggs hatch, she guards the young larvae and in some instances remains with them until they are adults, and sometimes even mates with her own sons. More recently, Wheeler (1923) made some

additional observations on Scleroderma macrogaster which he describes as follows:

"I was able not only to confirm all of Mr. Bridwell's interesting observations on the Hawaiian species of the genus but also to notice that the females may show an interest in her larvae while they are feeding. She licks them assiduously at times and seems to feed on the juices which exude from the prey around their heads. This is interesting in connection with the discussion on trophallaxis in Belonogaster..... Moreover, several females readily cooperated in paralyzing the same beetle larva and feed and oviposit together upon it without the slightest signs of mutual antagonism. The recently emerged males eagerly gnaw their way into the silken cocoons and fecundate the females while they are still in the pupal stage. Scleroderma is therefore adelphogamic, and since a single male will mate with several females and a single female with several males, it is also polygamous and polyandric."

Vespidae

The following subfamilies of the Vespidae, according to Wheeler (1928b), are also subsocial:

Masaridinae:	Ceramius lichtensteini
Eumeninae:	Synagris spiniventris
	Synagris cornuta

Eumeninae: *Odynerus tropicalis*
Eumenes maxillosus
Zethinae: *Zethus cyanopterus*
Zethusculus lobulatus

Wheeler cites Braun's observations on *Ceramius lichtensteini*, one of the Masaridinae, which occurs in the dry plains of Karroo, South Africa. It is of special interest, because it has adapted itself to living in very arid regions and has also become subsocial. The wasp hollows out small cavities along the main subterranean gallery which descends straight down to a depth of four or five feet, and then builds oval clay cells in these nests and deposits an egg in each one. Brauns is certain that the wasp feeds her larvae with flower-honey from day to day till ~~it is~~ they are full-grown, because he was never able to find stored pollen or honey in the cells with the larvae. The latter, when full-grown, construct a parchment-like cocoon within the clay cell, and ~~is~~ are thus protected against any periodical droughts.

As already pointed out, some of the Eumeninae practice mass-provisioning, while others feed their young from day to day. A species which employs the latter method of rearing its young is *Synagris*, which feeds her young larvae with caterpillars. According to Bequaert (1918), the habits of *Synagris spiniventris* have been studied by Roubaud.

Under normal conditions, this wasp supplies her nest with plenty of caterpillars and takes no further care of her offspring. On the other hand, when food is scarce for some reason or other, she remains with her egg until it hatches and then goes out and collects food as the larva needs it. When her larva has attained three-quarters of its full size, she provides it with the last provisions and seals it in its cell. Bequaert remarks, that "in *S. spiniventris*, progressive provisioning is still optional, and one observes all the transitional stages between this behavior and the normal provisioning in mass. The mother wasp shows great skill in adapting her habits to the external conditions."

S. cornuta, another species belonging to this genus, has gone a step further in the evolution of parental care. The female feeds her larva from day to day with pellets which ~~is~~ are made of a paste of ground-up caterpillars. This is a step toward the maternal care in incipient colonies of the social wasps, for ~~they feed their~~ here the mother feeds her young in precisely the same way.

Another wasp of the Belgian Congo (*Odynerus tropicalis*) according to Bequaert (1918), is known to feed her larva from day to day until it is full-grown. After oviposition, the female wasp waits till the egg hatches, and then brings the first provisions which consist of lepidopterous and coleopterous larvae. In this case the mother does not seal the cell until the larva is ready to pupate.

Still another member of the sub-family Eumeninae, Eumenes maxillosus, studied by Schuster (1911) in East Africa, also feeds her larva from day to day with paralyzed caterpillars.

The subfamily Zethinae includes at least two subsocial species, Zethus cyanopterus and Zethusculus lobulatus, both of which have been studied by Williams (cf. Wheeler, 1923). Zethus cyanopterus constructs a nest with one or several tubular cells and hence approaches the social paper-making wasps. Williams made a thorough study of this wasp and found that the female lays her egg loosely in the bottom of the cell. When the larva hatches from the egg, the mother fetches caterpillars and partly chews them up before feeding them to the young larva. While the latter is still small, the mother sleeps with it in its cell, but as soon as the larva is full-grown, she closes the cell and proceeds to build another.

Zethusculus lobulatus exhibits social habits which are similar to those of the preceeding species. The female, in this case, seems to sense the need of more food as the larvae increase in size, and provides them with larger and larger caterpillars as time goes on. If it rains, she protects the larvae by placing her body over the cell opening.

Sphecidae

There is only one species, *Aphilanthops frigidus*, belonging to this family, which provides its larva with food at intervals. Wheeler (1928a) found that this wasp prefers to make its burrow on a slightly sloping surface, usually digging to a depth of only six to eight inches, and ~~the mother~~ provisioning her nest with queen ants. ~~She carries the ant~~ The latter are carried under her body, and on reaching the nest, she usually enlarges the entrance so that the ant can easily be taken down. Wheeler observed the interesting fact that the female removes the wings of her prey before lowering it into the cell. Further data on the parental care of this species are contained in the following account by Wheeler (1928a):

"No eggs were to be found on such stored individuals, but in each of two nests a young larva was found in a small cell devouring a single ant, which had been cut in two at the petiole. The mother Aphilanthops was sitting in the burrow in each of these nests and in one of them there was a paralyzed ant in a chamber separated from the one in which the larva was feeding. Several older nests were excavated in which there was a single adult larva spinning its cocoon and surrounded by fragments of three or four queen ants. These conditions seem to me to prove that the Aphilanthops feeds her single larva from a store of several ants deposited in several cells. The egg is evidently laid on an isolated

ant which the mother wasp cuts in two in order that the larva may gain access to the nutritious contents of the thorax and gaster. Then the older ants are taken from storage and brought to the larva one by one as they are required, till all are consumed and the larva is ready to pupate...... If my interpretation of the feeding of the larva is correct, we have in Aphilanthops a very interesting condition intermediate between that of the great majority of solitary wasps, which first collect provisions and then lay an egg upon them and that of Bembex, which lays its eggs on a single fly and feeds the larva from day to day with fresh flies."

Bembicidae

The life-history and habits of several species belonging to the Bembicidae, or digger wasps, have been studied in considerable detail, chiefly by the Peckhams (1905), Hudson (1912), the Raus (1918), and Weed (1930). The species studied by these authors are the following: *Bembix nubilipennis*, *Bembix spinolae*, *Bicyrtes quadrifasciata*, and *Monedula punctata*. But since the parental care of all of these species is very similar, it seems best to discuss the behavior of only one, so as to avoid unnecessary repetition. Since the habits of *Bembix nubilipennis* have been studied ~~more~~ most extensively, it is probably best suited for this purpose.

The females of this species build their nests in the same locality, each wasp digging its own burrow until the latter is about ten inches long and some four or five inches below the surface. They make the lower end larger than the rest of the burrow, hollowing out a little chamber which is to be the nursery. The female lays an egg in the chamber and then leaves the burrow, filling the hole with sand. Having caught a small fly, she returns to the nest about the time the egg hatches, opens the tunnel, and places the fly within reach of the larva. As the larva grows, the mother catches larger and larger flies and feeds them to the larva until the latter is ready to spin its cocoon. She then closes the burrow and leaves her offspring to its own fate.

CONCLUSION.

The incipiently social or subsocial insects present a finely graded series of steps in the parental care which the female - rarely the male - bestows upon her offspring, one extreme being a complete indifference on the part of the female toward her eggs and young, and the other, a solicitude which equals, or, in some cases, even surpasses that of the Isoptera and Social Hymenoptera. Instances of parental care, e.g. where the female insect lays her eggs on food suitable to the hatching larvae and then departs, might be regarded as a potential nursing or fostering, for it readily becomes actual in a few species which manage to survive the hatching of their young and can therefore continue to feed and protect them.

Parental care on the part of the quasi-social insects discussed in the preceeding paragraphs illustrates the beginnings of ~~the~~ rudimentary family life, the perfection of which in the Isoptera and Social Hymenoptera have resulted in the complex insect societies of today.

Much more work needs to be done on the social habits of many species now thought to be solitary, for it is very probable that many of these, for example, the species comprising the genus Halictus, will be found to be social.

Boston University
Graduate School
A Digest of the Thesis

Quasi-social Behavior in the Insect World

by
Carl Edward Ludwig
(B.S.E., Fitchburg State Teachers College, 1935)

Submitted in partial fulfillment of the
requirements for the degree of
Master of Arts
1936

A Digest of the Thesis

Quasi-social Behavior in the Insect World.

This thesis represents an attempt to trace the solicitude which parents in the insect world display toward their young. The earliest reference to parental care among insects is apparently that of Goedaert (1662), who states that the mole-cricket (*Gryllotalpa gryllotalpa*) takes particular care of its eggs, raising up the nests in hot and dry seasons so that the young are near the surface of the earth and thus get the most benefit from the sun. On the other hand, when the air is cold and moist, the female ~~they~~ lowers the nest and guards her ~~The parents guard their~~ eggs and newly hatched young with the greatest of care.

A somewhat more advanced type of parental care has been discovered in a certain species of roach belonging to the family Blattidae. In this case, the mother carries her young larvae in a brood-chamber under her tegmina. The tegmina are large and convex and the abdomen above is concavely depressed, so that a chamber is formed for her young.

The Dermaptera, or earwigs, show a considerable degree of maternal solicitude. In the species of earwig studied, the female lays about fifty eggs in the ground, usually under a log or some other object. She rests over

her eggs, cleaning them from time to time, by rolling them around in her mouth. When the larvae are hatched they stay with the mother for a considerable period of time. Occasionally they seek food for themselves, but when doing so, never wander more than two or three feet from their mother. The ability of the female earwig to protect her young from enemies has been studied by Fulton (1924) and others. Fulton introduced carabid beetles into the nests of an earwig female and found that the mother never hesitated to attack the intruder and always did it with such vigor that the ground beetle invariably took flight.

A very similar behavior has been recorded by Imms (1913) in the case of the Embioptera, which comprise the so-called web-spinners. Embia major, one of the species, inhabits dense silken tunnels which it constructs beneath stones or logs. The female lives in close association with the eggs and young, protecting them so far as possible by means of her body. If she becomes alarmed and is driven away from her young, she returns sooner or later to take up her old position. When the young reach the second instar, they ~~exhibit a tendency to~~ wander from the immediate vicinity of the mother and construct adjacent tunnels for themselves. The whole colony is social in tendency and as many as twenty-one adult individuals have been found inhabiting a compound nest of interlacing passages.

Some twenty-three species of Hemiptera have been found to show a certain degree of subsocial behavior. The method employed in egg-laying, guarding the eggs, and watching the young until at least the second moult, is so similar that discussion of a representative case will suffice.

The female of Cantao ocellatus lays her eggs in rows on the under side of leaves. After oviposition, she places her abdomen over them, extends her antennae, and stays there without moving, never leaving the spot even for food. If approached, she moves her legs and antennae, and if touched with an object, she bends her body in the direction of the threatening object. After the eggs have hatched, the nymphs remain under the body of the mother until they have undergone two moults. Then they begin to move about and seek food for themselves, the mother remaining on the empty egg-mass until she dies of starvation.

Among the beetles of the family Scarabaeidae, the male and female of Copris lunaris associate in pairs. They excavate an earthe~~r~~n chamber which they fill with ellipsoidal balls of dung, in each of which an egg is deposited. These are guarded while the larva are devouring the food thus provided. When the young become adults, they are accompanied to the surface of the ground by the parents.

Other species of Copris, and allied dung beetles, exhibit very similar parental behavior.

One of the more recently discovered examples of quasi-social habits is that of ~~afforded by~~ certain species of the family Silvanidae. Wheeler (1923) found them living along with their brood, in the hollow petioles of young Tachigalia trees in British Guiana. Both the adults and larvae feed on the nutritive tissue within the petioles and also on the secretion given off by coccids which enter the cavity. The young pupate in the petiole and as soon as they become adults, they also begin to lay eggs, and, eventually, the petiole contains ~~consists of~~ six or seven generations of this beetle. When the chamber becomes over-crowded, some of the beetles vacate and start a new colony in a different petiole of the same or another young Tachigalia.

A still higher type of subsocial behavior is that found among the Hymenoptera. No other insect Order offers a better illustration of the probable evolution of the family. Some species of Hymenoptera, for example most of the saw-flies and wood-wasps merely deposit their eggs in a suitable food plant. Others, like the spider-wasps and solitary bees collect and store food for their offspring, while still others, for example the Bembicidae, show a solicitude for their offspring which is not surpassed by ants, wasps, and bees, or even by altricial birds.

LITERATURE CITED

Ballard, E., and Holdaway, F. G.
1926. The life-history of *Tectacoris lineola* and its connection with internal boll rots in Queensland. Bull. Ent. Res., Vol. 16, pp. 329-346, 2 pls.

Barber, H. G.
1925. Maternal care shown by certain Hemiptera. Journ. New York Ent. Soc., Vol. 33, p. 116.

Beamer, R. H.
1930. Maternal instinct in a membracid (*Platycotis vittata*). Ent. News, Vol. 41, pp. 330-331, 1 pl.

Bennett, C. B.
1904. Earwigs (*Anisolabis maritima*). Psyche, Vol. 11, pp. 49-53, 2 figs.

Bequaert, J.
1918. A Revision of the Vespidae of the Belgian Congo Based on the Collection of the American Museum Congo Expedition, with a List of Ethiopian Diplopterous Wasps. Bull. Am. Museum of Nat. Hist., Vol. 39, pp. 1-384, 6 pls., 267 figs.

————
1935. Presocial Behavior Among the Hemiptera. Bull. Brooklyn Ent. Soc., Vol. 30, No. 5, pp. 177-191.

Bridwell, J. C.
1920. Some Notes on Hawaiian and other Bethylidae, with the Description of a New Genus (Second Paper). Proc. Hawaiian Ent. Soc., Vol. 4, pp. 291-314.

Bueno, J. R. de la Torre.
1935. Notes on *Gragaphia tiliae*. Bull. Brooklyn Ent. Soc., Vol. 30, p. 78.

Caudell, A. N.
1920. Zoraptera not an Apterous Order. Proc. Ent. Soc. Washington., Vol. 22, pp. 84-97, 1 pl.

Cleveland, L. R.
1934. The Wood-feeding Roach *Cryptocercus*, its Protozoa, and the Symbiosis between Protozoa and Roach. Mem. Am. Acad. Arts and Sciences, Vol. 17 (No. 2), 60 pls., 40 figs.

Dodd, F. P.
1904. Notes on maternal instinct in Rhynchota. Trans. Ent. Soc. London, pp. 483-486. 1 pl., 1 fig.

————
1916. Observations on various insects in North Queensland. Trans. Ent. Soc. London, Proc., pp. xxv-xxvii.

Fabre, J. H.
1911. The life and love of the insect. (Trans. by A. Teixeira de Mattos). Black, London.

————
1918. The Sacred Beetle and Others. Dodd, Mead and Company, New York.

Fink, D. E.
1915. The eggplant lacebug. Bull. U. S. Dept. Agric., No. 239, 7 pp., 6 pls.

Froggatt, W. W.
1918. Notes on Australian Saw-flies (Tenthredinidae). Proc. Linn. Soc. N. S. Wales, Vol. 43, pp. 668-672.

Fulton, B. B.
1924. Some Habits of Earwigs. Ann. Ent. Soc. Amer., Vol. 17, pp. 357-367.

Goedaert, J. (cf. Reuter, 1913).
1662. ~~Metamorphosis et historia naturalis~~. ~~Insectorum~~, ~~1, pp. 168-171~~.

Herbst, J. F. W.
1786. (Translation of Modeer's paper of 1764). Neues Magazin f. die Liebhaber der Entomologie (edited by J. C. Fuessly), Vol. 3, pp. 64-67.

Hoffmann, W. E.
1924. Biological notes on *Lethocerus americanus*. Psyche, Vol. 31, pp. 175-183.

Hopkins, A. D.
1898. On the History and Habits of the Wood Engraver Ambrosia Beetle *Xyleborus xylographus*, *Xyleborus saxeseni*, with brief Descriptions of Different Stages. Canad. Ent., Vol. 30, pp. 21-29, 2 pls.

Hubbard, H. G.
1897. The Ambrosia Beetles of the United States. Bull. 7 (N.S.) Div. Ent. U. S. Dept. Agric., pp. 9-30, 34 figs.

———
1906. Ambrosia Beetles. Yearb. U. S. Dept. Agric., pp. 421-430, 7 figs.

Hudson, W. H.
1912. The Naturalist in La Plata. J. M. Dent & Sons, London.

Hussey, R. F.
1934. Observations on *Pachycoris torridus*, with Remarks on Parental Care in other Hemiptera. Bull. Brooklyn Ent. Soc., Vol. 29, No. 4, pp. 133-145.

Imms, A. D.
1913. On *Embia major* sp. nov. from the Himalayas. Trans. Linn. Soc. London, Zool. (2), Vol. 11, pp. 167-195, 3 pls., 6 figs.

———
1931. Social Behavior in Insects. The Dial Press, N. Y.

Jones, D. W.
1917. The European Earwig and its Control. Bull. No. 566, U.S. Dept. Agric., 12 pp., 8 figs.

Keys, J. H.
1895. Some remarks on the habits of *Aëpophilus bonnairii*. Ent. Mo. Mag., Vol. 6, pp. 135-137.

———
1914. Some further remarks on *Aëpophilus bonnairii*. Ent. Mo. Mag., Vol. 25, pp. 284-285.

Kirkaldy, G. W.
1903. Upon maternal solicitude in Rhynchota and other non-social insects. Entomologist, Vol. 36, pp. 113-120.

———
1904. Upon maternal solicitude in Rhynchota and other non-social insects. Smithsonian Report for 1903, pp. 577-585.

Lewis, R. H.
1836. Case of Maternal Attendance on the Larva by an Insect of the Tribe Terebrantia, belonging to the genus Perga, observed at Hobarton, Tasmania. Trans. Ent. Soc. London, Vol. 1, pp. 232-234.

McClure, H. E.
1932. Incubation of bark-bug eggs (Aradidae). Ent. News, Vol. 43, pp. 188-189.

Melander, A. L.
1902. Two New Embiidae. Biol. Bull., Vol. 3, pp. 16-26, 4 figs.

Montrouzier, A.
1855. Essai sur la faune de l'ile de Woodlark on Mouion. Ann. Soc. Sci. Phys. Nat. Agric. Lyon, Vol. 7, No. 2, pp. 1-114 (see pp. 91-92).

Morse, A. P.
1920. Manual of the Orthoptera of New England. Proc. Boston Soc. Nat. Hist., Vol. 35, pp. 197-556, 20 pls.

Myers, J. G.
1921. The life-history of some New Zealand insects. Trans. New Zealand Institute, Vol. 53, No. 1, pp. 235-237, 1 pl.

Ohaus, F.
1899-1900. Bericht über eine entomologische Reise nach Zentralbrasilien. Stettin. Ent. Zeitg., Vol. 60, pp. 204-245.

Peckham, G. W. and Peckham, E. G.
1905. Wasps, social and solitary. Houghton Mifflin & Co., Boston.

Perkins, R. C. L.
1897. Notes on Oligotoma insularis (Embiidae), and its immature Conditions. Ent. Mo. Mag., Vol. 8, No. 2, pp. 56-58.

Rau, P., and Rau, N.
1918. Wasp Studies Afield. Princeton Univ. Press, Princeton, N. J.

Reuter, O. M.
1913. Lebensgewohnheiten und Instinkte der Insekten. R. Friedländer & Sohn, Berlin.

Schuster, L.
1911. *Eumenes maxillosa*. Zeitschr. wiss. Insektenbiol., Vol. 7, pp. 27-28.

Schwarz, E. A., and Barber, H. S.
1921. Descriptions of New Species of Coleoptera. Zoologica, Vol. 3, pp. 189-193.

Shelford, R.
1906. Studies of the Blattidae. Trans. Ent. Soc. London, Vols. 5-7, pp. 487-519, 1 pl.

Snyder, T. E.
1924. Adaptations to Social Life. Smithson. Misc. Coll., Vol. 76, No. 12, 14 pp., 3 pls.

Stäger, R.
1919. Erlebnisse mit Insekten. Rascher & Co., ~~Verlag~~, Zürich.

Step. E.
Marvels of Insect Life. Huschinson & Co., London.

Uvarov, B. P.
1928. Locusts and Grasshoppers. Imperial Bureau of Entomology, London.

Weed, C. M.
1930. Insect Ways. D. Appleton and Co., New York.

Weiss, H. B.
1919. Notes on *Gargaphia tiliae*, the linden lace-bug. Proc. Biol. Soc. Wash., Vol. 32, pp. 165-168.

Westwood, J. O.
1837. Characters of *Embia*, a Genus of Insects allied to the White ants (Termites), with Descriptions of the Species of which it is composed. Trans. Linn. Soc. London, Vol. 17, pp. 369-375, 1 pl.

Wheeler, W. M.
1921. A Study of Some Social Beetles in British Guiana and of their relations to the ant-tree *Tachigalia*. Zoologica, Vol. 3, pp. 35-126, 5 pls., 12 figs.

——————
1923. Social Life Among the Insects. Harcourt, Brace & Co., New York.

Wheeler, W. M.
1928a. Foibles of Insects and Men. Alfred a Knopf, N. Y.

____________ 1928b. The Social Insects. Harcourt, Brace & Co., N. Y.

Wheeler, W. M. and Bailey, I. W.
1920. The Feeding Habits of Pseudomyrmine and other Ants. Trans. Amer. Phil. Soc. N. S., Vol. 22, pp. 235-279, 5 pls., 6 figs.

BOSTON UNIVERSITY
1 1719 02549 1913